

CHAPTER 2

MARION LAKE STRATIGRAPHY¹

As a first exploratory look at the chironomid stratigraphy in a British Columbia lake, Marion Lake in the University of British Columbia Research Forest was selected for study. This initial investigation would allow a comparison of chironomid successional patterns in British Columbia with those documented elsewhere in North America and Europe.

Extensive ecological (Efford and Hall, 1975; Hall and Hyatt, 1974) and palaeoecological (Mathewes, 1973; Mathewes and Heusser, 1981; Wainman and Mathewes, 1987) research has been conducted at Marion Lake. The extant chironomid fauna is well documented (Hamilton, 1965), and the lake is of comparable size to other North American sites from which detailed postglacial chironomid stratigraphic records have been obtained (Lawrenz, 1975; Walker and Paterson, 1983). The faunas of small lakes are likely to be most responsive to climatic changes. Also, a complete postglacial sediment core was available for study. The lake is unusual in having large stream and spring-water inputs.

Study Area

Located about 50 km east of Vancouver, British Columbia, in the University of British Columbia Research Forest (Fig. 2.1), Marion Lake (49° 19'N, 122° 33'W) occupies a valley depression in the Coast Mountains at 304 m above sea level. The area is exposed to a mediterranean type climate. Although summer precipitation is similar to that in much of southern Canada, summer temperatures are slightly cooler, and winter is

¹ This chapter is largely adapted from a previously published account (Walker and Mathewes, 1987a).

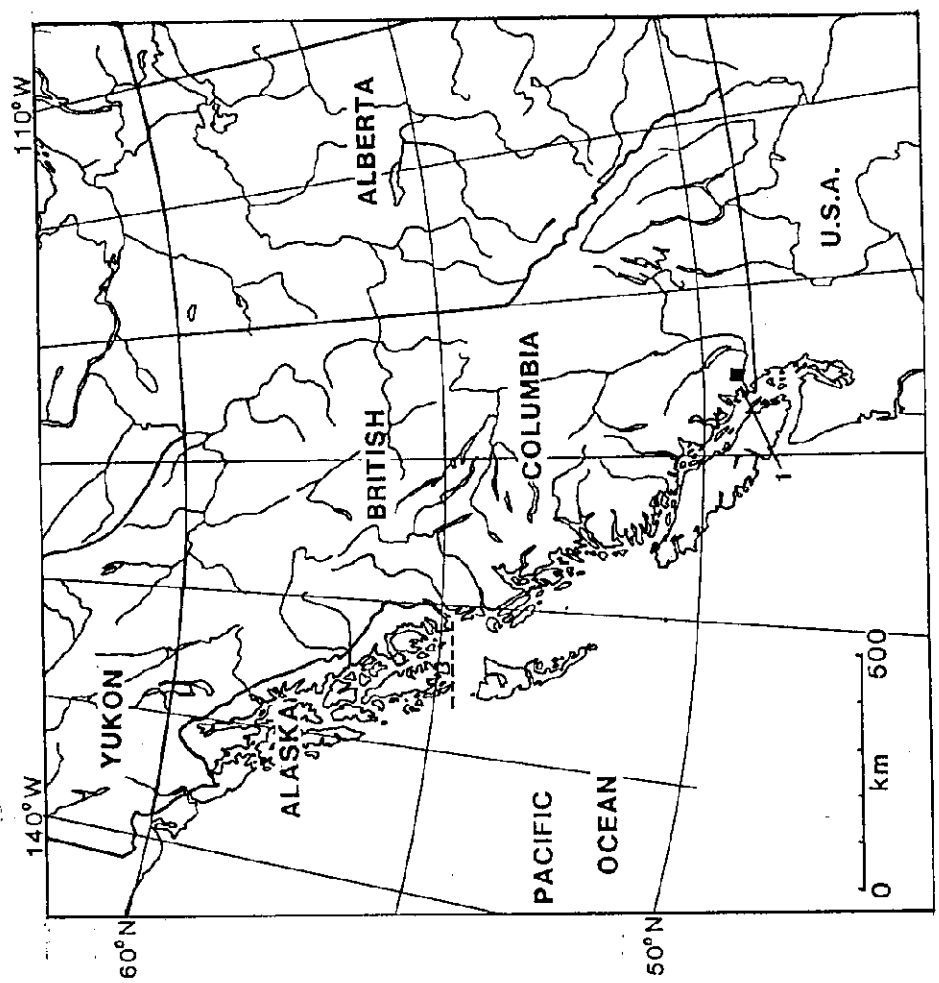
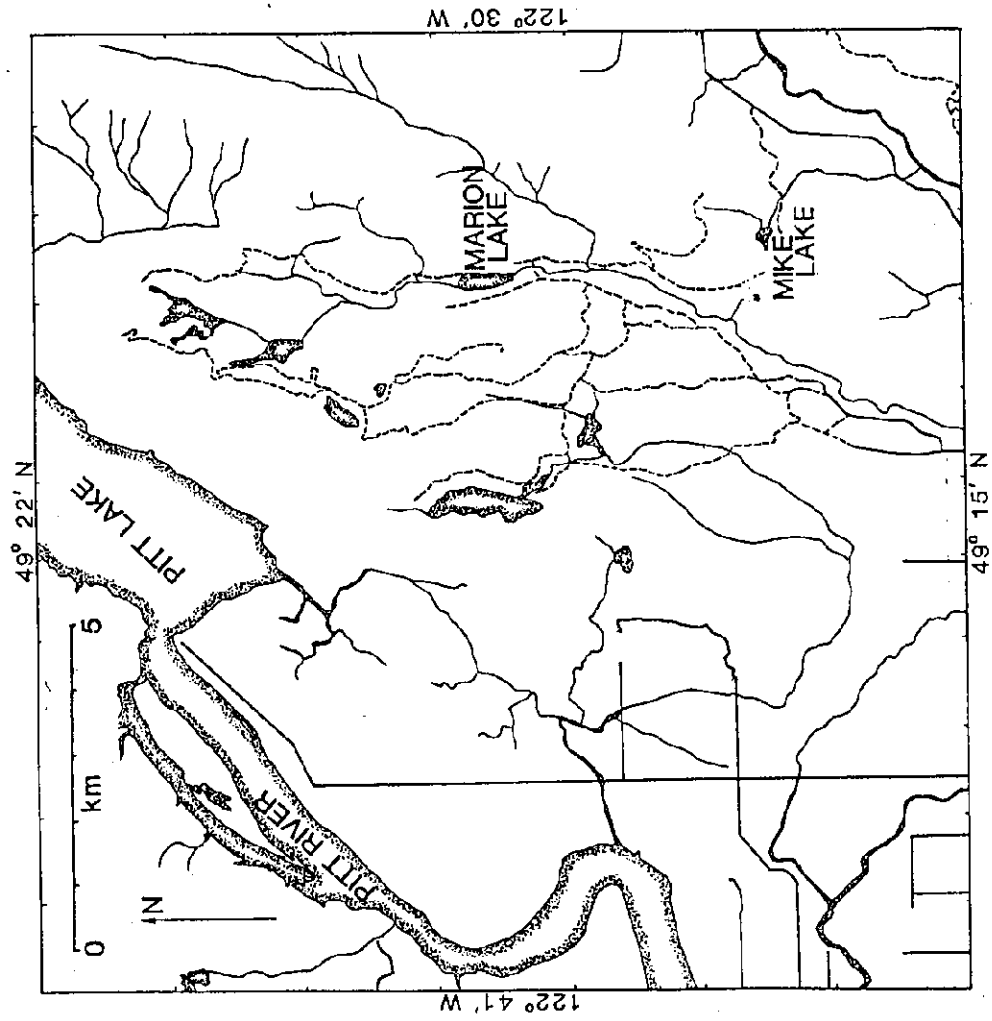


Figure 2.1 Location of Marion Lake in the University of British Columbia Research Forest, near Maple Ridge, British Columbia, Canada.

comparatively warm and wet (Table 2.1). The lake has an area of 13.3 ha and maximum depth of approximately 6 m (Hamilton, 1965). The catchment encompasses 15 km², with tributary streams extending to at least 500 m above lake level. Perhaps owing to the rapid flushing of Marion Lake following frequent rains, little stratification of the water column is apparent. Temperatures at 5.0 m depth can exceed 17°C during summer, whereas winter temperatures approach 2°C (Hamilton, 1965). Efford (1967) notes, however, that water as cold as 9.5°C can be found during summer over one large spring in the lake bottom. As a result of the high precipitation (2500 mm) and base-poor plutonic bedrock (Roddick, 1965), Marion Lake is a weakly-acidic to circum-neutral (pH 5.9 to 7.4), oligotrophic, softwater lake, typical of those along British Columbia's mainland coast.

The conifer-dominated forests of the (wetter) coastal Western Hemlock Zone (Krajina, 1969) that surround the lake have been extensively disturbed by fires and logging. The present forest consists primarily of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and red alder (*Alnus rubra* Bong.).

Palynological investigations (Fig. 2.2) reveal the postglacial forest history of Marion Lake's catchment (Mathewes, 1973). Climatic interpretations are available as established by pollen/climate transfer functions (Mathewes and Heusser, 1981). The earliest sediment ($\geq 12,000$ yr B.P.; ≥ 8.85 m) is dominated by clay and contains a significant non-arboreal pollen component including willow (*Salix* L.) and soapberry (*Shepherdia canadensis* (L.) Nutt.). Forests were then rapidly established at the site. All subsequent sediments, excluding the Mazama volcanic ash layer (6800 yr B.P.: Bacon, 1983), are highly organic, containing much allochthonous plant debris. Early forests (12,000 - 10,000 yr B.P.) included lodgepole pine (*Pinus contorta* Dougl.), balsam fir (*Abies* Mill.), spruce (*Picea* A.Dietr.), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and alder, suggesting a

Table 2.1. Climatic summary (1951-1980) for Loon Lake (49°18'N, 122°35'W; 354 m elev.), University of British Columbia Research Forest, Haney, British Columbia.

Mean Daily Temperature	
Coldest Month (Jan)	0.5°C
Warmest Month (Jul)	16.3
Precipitation	
Rain: Annual	2459.1 mm
Wettest Month (Dec)	343.3
Driest Month (Jul)	86.7
Snow: Annual	195.2 cm
Frost-free Period	199 d
Degree-days	
Above 0°C	3092.7°C·d
Above 5°C	1633.7

(Environment Canada, 1982)

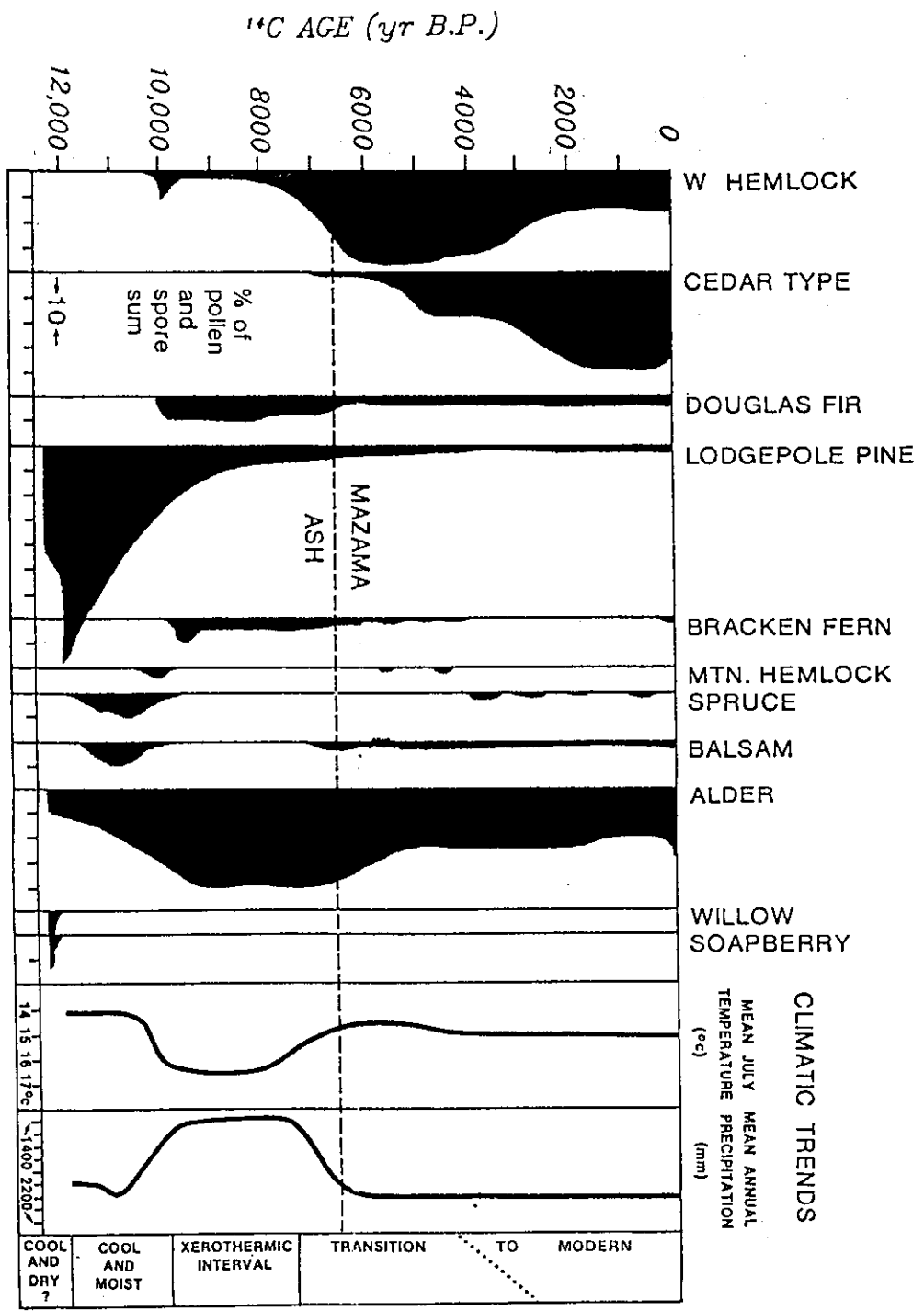


Figure 2.2 Summary diagram of postglacial pollen stratigraphy at Marion Lake, B.C. (adapted from Mathewes, 1985).

cool moist climate. Maximum proportions of Douglas-fir, alder, and bracken (*Pteridium aquilinum* (L.) Kuhn.) palynomorphs between 10,000 and 7000 yr B.P. imply a warm dry climate, described as a xerothermic interval (Mathewes and Heusser, 1981) with increased fire frequency (Mathewes, 1985). Post-Mazama maximum frequencies of western hemlock and western red cedar indicate a shift towards the present cooler and wetter climate. These patterns of forest development and the climatic inferences accord well with evidence from other sites in the same region (Mathewes, 1985).

Methods

A 5-cm-diameter sediment core was collected at the point of maximum depth (ca. 6 m) in Marion Lake using those methods described by Mathewes (1973). Because this core was taken close to one previously studied palynologically (Mathewes, 1973) the stratigraphy of this 8.95-m core is identical to that described by Mathewes (1973). A reliable stratigraphic correlation of the two records is therefore possible.

One millilitre samples of sediment were normally used for chironomid analysis. Larger samples (≤ 30 mL) were occasionally necessary, especially for the basal clay (≥ 8.85 m). The samples were spaced at approximately 1.0 m intervals, except in sediments below 8.0 m and near the Mazama ash (6.1 m) where rapid faunal changes were expected. In these instances, samples were more closely spaced. Samples were deflocculated in hot 10% KOH and sieved through a .075 mm mesh. The sediment retained in the sieve was washed into a beaker and later examined in a Bogorov counting tray (Gannon, 1971) at a magnification of 50X for fossil chironomids. All fossil Chironomidae were mounted on microscope slides in Permount[®] and retained for identification. Counts per sample averaged 91.6 ± 12.2 (S.E.) chironomid head capsules, with a minimum of 25.5 and maximum of 203.5.

Head capsules were identified principally with reference to the work of Hamilton (1965), Oliver and Roussel (1983a) and Wiederholm (1983). Nomenclature follows Wiederholm (1983). Because most appendages were separated from the head capsules, it was not possible to provide all identifications at the generic level and few at the species level. Thus, several broader taxonomic categories (e.g. *Corynoneura* Winnertz/*Thienemanniella* Kieffer, *Cricotopus* v.d.Wulp/*Orthocladius* v.d.Wulp/*Paratrichocladius* Santos Abreu, *Tanytarsus* s.lat.) have been designated. Details regarding the identification of individual taxa, including diagnostic characters, illustrations, and species likely to be included in each group are provided as an appendix to this thesis.

The chironomid diagrams were been plotted using the pollen-plotting package MICHIGRANA developed by R. Futyma and C. Meachum. Head capsule influx estimates were calculated assuming constant sedimentation rates between radiocarbon-dated levels. Zonation of the diagrams is subjective.

Results

The counts of head capsules are presented as percentages² (Fig. 2.3), as well as total influx³ (Fig. 2.4). Although ideally representing the abundance of individual taxa, interpretation of influx data is limited by the possibility of sediment focusing (Davis *et al.*, 1984) concentrating littoral head capsules in the less turbulent sublittoral region (Iovino, 1975). Thus total influx values are presented, but not influx estimates for individual chironomid taxa.

² For individual samples, the proportion of each taxon has been calculated as a percentage, of the total number of chironomid head capsules.

³ Total influx refers to the rate at which head capsules of all chironomid species are being deposited and preserved in the sediments. Influx is reported as the number of head capsules deposited per cm² per year (hc·cm⁻²·yr⁻¹).

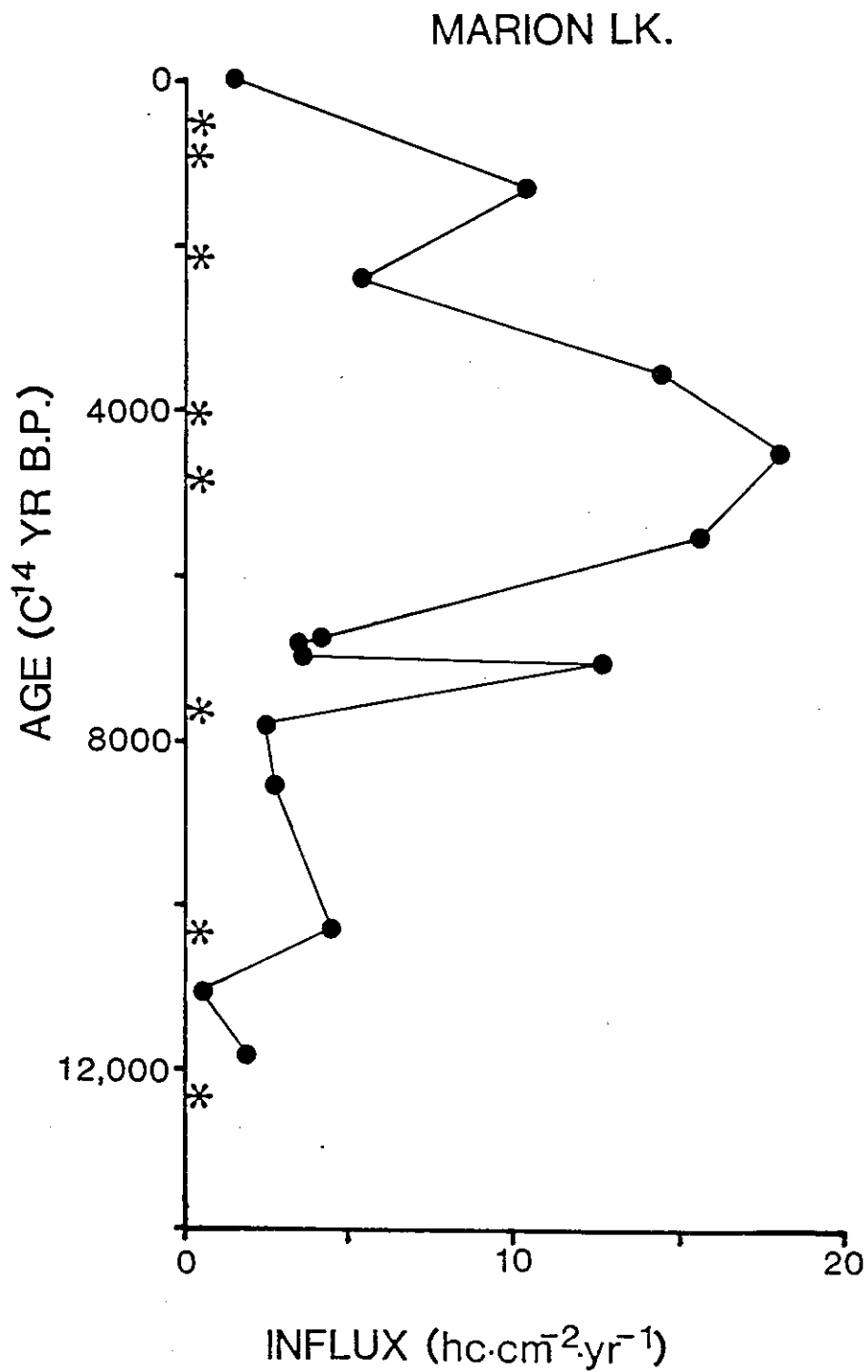


Figure 2.4 Total chironomid influx at Marion Lake, B.C. (*-indicate ¹⁴C-dated levels - from Mathewes, 1973).

Chironomid taxa have been assigned to ecological groups, but given the broad ecological range of most genera, these designations must be considered approximate. The "cold-stenothermous" taxa are commonly regarded as profundal species at temperate latitudes, but may extend into shallower habitats at high elevation or latitude. For example, *Stictochironomus rosenscholdi*, considered a temperate profundal midge (Sæther, 1979), has been collected emerging among macrophytes in arctic Alaskan lakes and ponds (Butler *et al.*, 1981; Hershey, 1985a). Those taxa designated as "rheophilous" were not recorded as common components of Marion Lake's extant fauna (Hamilton, 1965), and are known to be associated with stream habitats in other regions (Coffman and Ferrington, 1984; Wiederholm, 1983). *Cricotopus/Orthocladius/Paratrichocladius* is the only taxon of the "rheophilous" group commonly recorded as a fossil in British Columbia lakes with no significant stream input (see chapter 5).

Most of the remaining chironomids are common in littoral environments. Only *Chironomus decorus* Johannsen, *C. rempeli* Thienemann, *Procladius* sp.A, *Psectrocladius* (*Monopsectrocladius*) sp.B, and *Sergentia* sp.A were noted by Hamilton (1965) as being most common in deep-water areas of Marion Lake, suggesting a preference for profundal environments. Both *Chironomus* and *Sergentia* are well known as profundal inhabitants of other lakes.

The fossil chironomid record may be divided into 3 zones. The lowermost zone (8.95 - 8.20 m) encompasses the late-glacial sediments deposited between *ca.* 12,000 and *ca.* 10,000 yr B.P. (Mathewes and Heusser, 1981). The second zone (8.2 - 6.1 m) was deposited between 10,000 and 6800 yr B.P. The third zone, containing sediments above the Mazama ash (6.1 to 0.0 m), spans the period from 6800 yr B.P. to the present day.

Late-glacial assemblages

Chironomid assemblages in the late-glacial sediments are distinguished by low influx⁴ (ca. 2.0 hc-cm⁻²-yr⁻¹) (Fig. 2.4) and by the prevalence of *Heterotrissocladius*, *Parakiefferiella* sp.A, *Protanypus*, and *Stictochironomus* (Fig. 2.3). Although the clays forming the base of this zone bear lower concentrations of head capsules, they have not yielded a distinctive fossil fauna.

Heterotrissocladius and *Protanypus* Kieffer are cold-stenothermous taxa which at temperate latitudes are mostly restricted to the profundal sediments of deep, oligotrophic lakes (Sæther, 1975b, c). At higher latitudes they may become more common in shallow waters. *Stictochironomus* Kieffer is also a resident of northern lakes (Hershey, 1985a, b; Moore, 1978, 1980; Danks, 1981) and a common deep-water component of temperate oligotrophic and mesotrophic water (Sæther, 1975a, 1979). Although some *Stictochironomus* species do occur in warm waters, the common species in British Columbia is restricted to cold environments (see Chapter 5).

Parakiefferiella sp.A is probably identical to Sæther's (1970) "genus near *Trissocladius*". This taxon presently inhabits the deep-water sediments of two large lakes in British Columbia's Okanagan Valley (Sæther, 1970; Sæther and McLean, 1972). It appears identical to larvae collected by M. Ouellet from Manicouagan Reservoir, a large oligotrophic lake in northern Québec, and to larvae collected by S. Mozley from the Alaskan north slope (D.R. Oliver, pers. comm.). Hare (1976) reports this taxon as abundant in the deep, oligotrophic waters of Parry Sound, Lake Huron, and as inhabiting several small lakes at alpine and subalpine sites in Banff National Park, Alberta.

⁴The abbreviation "hc" is used throughout this thesis as an alternative to "head capsules".

A rare but significant taxon in the late-glacial sediments is *Pseudodiamesa* Goetghebuer. Like the preceding taxa, it is characteristic of very cold, waters, including ponds on glacier surfaces, oligotrophic lakes, and alpine streams (de March *et al.*, 1978; Elgmork and Sæther, 1970; Minns, 1977; Oliver, 1976). *Pseudodiamesa* is principally distributed in arctic and alpine regions (Downes, 1964), although Beck (1980) provides one record from Tennessee. D.R. Oliver (pers. comm.) notes the occurrence of *Pseudodiamesa* in Ontario springs.

Local extinction of *Parakiefferiella* sp.A and *Stictochironomus* appears to have occurred in the interval encompassing the 8.1 and 8.3 m depths, dated approximately 10,000 yr B.P. *Heterotrissocladius* and *Protanypus* occur above 8.1 m, but constitute a much reduced faunal element.

Holocene assemblages

Unlike the late-glacial fauna, the Holocene fauna bears a high proportion of *Tanytarsus* s.lat. remains. Although I divide the Holocene with a zone boundary at the Mazama Ash, the gradual changes in the Holocene do not provide a marked distinction between the fauna immediately above and below the ash. However, this boundary does facilitate description of observed faunal changes.

Some taxa appear relatively more abundant in the pre-Mazama sediments. The high pre-Mazama proportion of rheophilous taxa, including *Corynoneura/Thienemanniella*, *Eukiefferiella* Thienemann/*Tvetenia* Kieffer, *Orthocladius* (*Symposiocladius*) *lignicola* Kieffer, *Parametriocnemus* Goetghebuer group and *Stilocladius* Rossaro, may reflect low production of lake Chironomidae, rather than a higher influx of chironomids from the in-flowing stream (Figs. 2.3, 2.4).

Littoral taxa (e.g. *Corynocera* nr. *ambigua* Zetterstedt, *Pagastiella* cf. *ostansa* Webb, *Parakiefferiella?* cf. *triquetra* (Chernovskii), *Psectrocladius* Kieffer, *Stempellinella* Brundin, *Tribelos* Townes) are more abundant in sediments above the Mazama ash. Although abundant between 4.0 m and 1.0 m, *Corynocera* nr. *ambigua* is rare in pre-Mazama sediments, as well as being absent from the present lake (Hamilton, 1965). The influx of head capsules increases sharply (Fig. 2.4) in post-Mazama sediments. In part this may reflect greater chironomid production as the lake shallowed and littoral habitat increased. On the other hand, head capsules may be concentrated at sublittoral sites by offshore displacement of head capsules. Head capsules resuspended from the turbulent littoral environment can be transported to deeper water (Iovino, 1975).

The deposition of Mazama ash does not appear to have had great effect upon the chironomid fauna. Perhaps, such a response would be evident at another lake where laminated sediments provide greater time resolution. Curiously however, Simuliidae (blackfly) larval remains are abundant, on a relative basis, during three periods in which soil disturbance and consequently stream sediment loads may have been great. These periods include the late-glacial (solifluction, incomplete forest cover), the period subsequent to ash deposition, and the recent settlement era (logging and increased fire frequency). Unfortunately, because this is a relative increase, and because it is difficult to accurately assess the rate of sediment deposition, it is not clear whether the apparent abundance of Simuliidae is real, or is instead caused by a decrease in total chironomid influx.

Discussion

To what factors might these variations in the chironomid fauna be attributed? For those changes occurring at or near the Pleistocene/Holocene boundary, two explanations are possible, temperature changes and trophic alterations. Subsequent Holocene changes

may have resulted largely from the gradual shallowing of Marion Lake. It is the possible influence of the late-Pleistocene climatic amelioration which will constitute the focal point of this discussion.

Chironomidae, to date, have been employed principally as indicators of the trophic status of lakes. *Chironomus* characterizes the deep-water benthic communities of eutrophic waters; *Heterotrissocladius*, associated with several Tanytarsini, is considered indicative of oligotrophic conditions. It is, however, important to note that the "*Heterotrissocladius*" fauna⁵ includes cold-stenothermous types, such as *Protanypus*. Although typically residents of very deep water at temperate latitudes, some members of the *Heterotrissocladius* community may inhabit shallower waters in arctic, subarctic, and alpine lakes (Hershey, 1985a; Hofmann, 1971a, 1983a; Moore, 1978; Sæther, 1975b, c).

Was the demise of the late-glacial *Heterotrissocladius* fauna a result of increasing summer water temperatures? Was its demise associated with an increase in lake productivity? Both events are likely to have occurred, and both may have contributed to this faunal change.

During Marion Lake's earliest development (>12,000 yr B.P.), cold water temperatures may have been maintained by meltwater from persistent valley glaciers. After ca. 12,000 yr B.P., sediments suggest low inorganic sediment influx, indicating disappearance of local ice and stabilization of adjacent slopes by forest vegetation. Subsequently, summer water temperatures would have increased with ameliorating climate. Warmer water, after ca. 10,000 yr B.P., would have restricted cold-stenothermous organisms to the deepest portions of the lake (if thermally stratified) and to the vicinity of cold springs. However, considering the rapid flushing which occurs at Marion Lake

⁵In this manuscript, the "*Heterotrissocladius*" fauna will be considered to include *Heterotrissocladius*, *Parakiefferiella* sp.A, *Protanypus*, and *Stictochironomus*. It is probably a regional analogue to the fauna in Brundin's (1958) "*Heterotrissocladius subpilosus*" lakes.

(Efford, 1967), it is debatable whether or not a stable, cold, hypolimnetic environment ever persisted throughout the summer.

Given the lake's large littoral extent, and essentially polymictic nature, most fossil Chironomidae deposited at the coring site are probably from littoral areas subject to warm summer temperatures. Present summer temperatures near the maximum depth attain 17° C (Hamilton, 1965). Sæther (1975b) reports that in Europe, *Heterotrissocladius marcidus* (Walker), the most warm-adapted member of the genus, is restricted to waters colder than 18° C. Clearly, Marion Lake provides marginal conditions. Increased water temperatures would also promote colonization by warm-adapted species. Thus warm water would produce a relative decline in the *Heterotrissocladius* fauna by restricting the cold-stenothermous species to those limited regions of the lake where cold spring water or bottom water prevailed throughout the summer, and by facilitating colonization by other chironomids and competitor organisms.

Trophic changes must also have occurred, but most likely in response to rising summer temperatures. By regulating growth rates and other biological processes, temperature can directly influence both autochthonous and allochthonous productivity. Analyzing data from 55 International Biological Program studies, Brylinsky and Mann (1973) concluded that primary production, at the global scale, depends mostly upon latitude, altitude, length of growing season, and mean air temperature. In addition, the nutrient supply and hence production is regulated by nutrient release from the catchment. Higher temperatures facilitate more rapid chemical weathering of parent materials, releasing scarce nutrients such as phosphorus.

Therefore, temperature, through both direct effects upon organisms and indirect regulation of lake productivity, could account for the observed Pleistocene to Holocene faunal changes. Indeed, pollen/climate transfer functions (Mathewes and Heusser, 1981)

indicate a rapid climatic warming at Marion Lake spanning the Pleistocene/Holocene boundary. Although significant water level fluctuations might produce faunal changes of the sort involved here, neither the present study nor Mathewes' (1973) study suggest water level fluctuations sufficient to explain these changes.

At this point comparison of these results with earlier reports is instructive (Fig. 2.5). Most early investigations (e.g. Goulden, 1964; Megard, 1964; Stahl, 1959) of postglacial chironomid stratigraphy suffer from inadequate dating and poor taxonomic resolution, so they are of little use in this analysis. Most recent, detailed investigations (Günther, 1983; Hofmann, 1971a, 1983a; Lawrenz, 1975; Schakau and Frank, 1984; Walker and Paterson, 1983) document *Heterotrissocladius* at maximum abundance during the late Pleistocene, when cold air and water temperatures are thought to have prevailed at each study site. *Heterotrissocladius* is extremely rare or entirely absent during postglacial time. It is compelling, therefore, to invoke climate as the principal factor regulating occurrence of the *Heterotrissocladius* community.

In a recent analysis of succession in a shallow North German lake, Hofmann (1983a) suggests that changing trophic conditions do not alone account for the observed successional patterns. Climatic conditions were also likely to be involved. Similarly, Brodin (1986) states, "The reasons for the almost complete elimination of cold-stenothermal species and the marked dominance of eutrophic species characteristic of the temperate climate zone in all shallow lakes at the beginning of the postglacial period seem to be mainly the distinctly warmer climate and an intrinsic capacity for highly productive conditions in these lakes, ..." I also believe climatic variations are necessary to account for the early chironomid succession in Marion Lake. When I consider the strong similarity of chironomid profiles within a restricted geographic area, as in Germany (Günther, 1983; Hofmann, 1971a, 1983a) or New Brunswick (Walker and Paterson, 1983) it is clear that the lake faunas are not reacting independently. A regional influence,

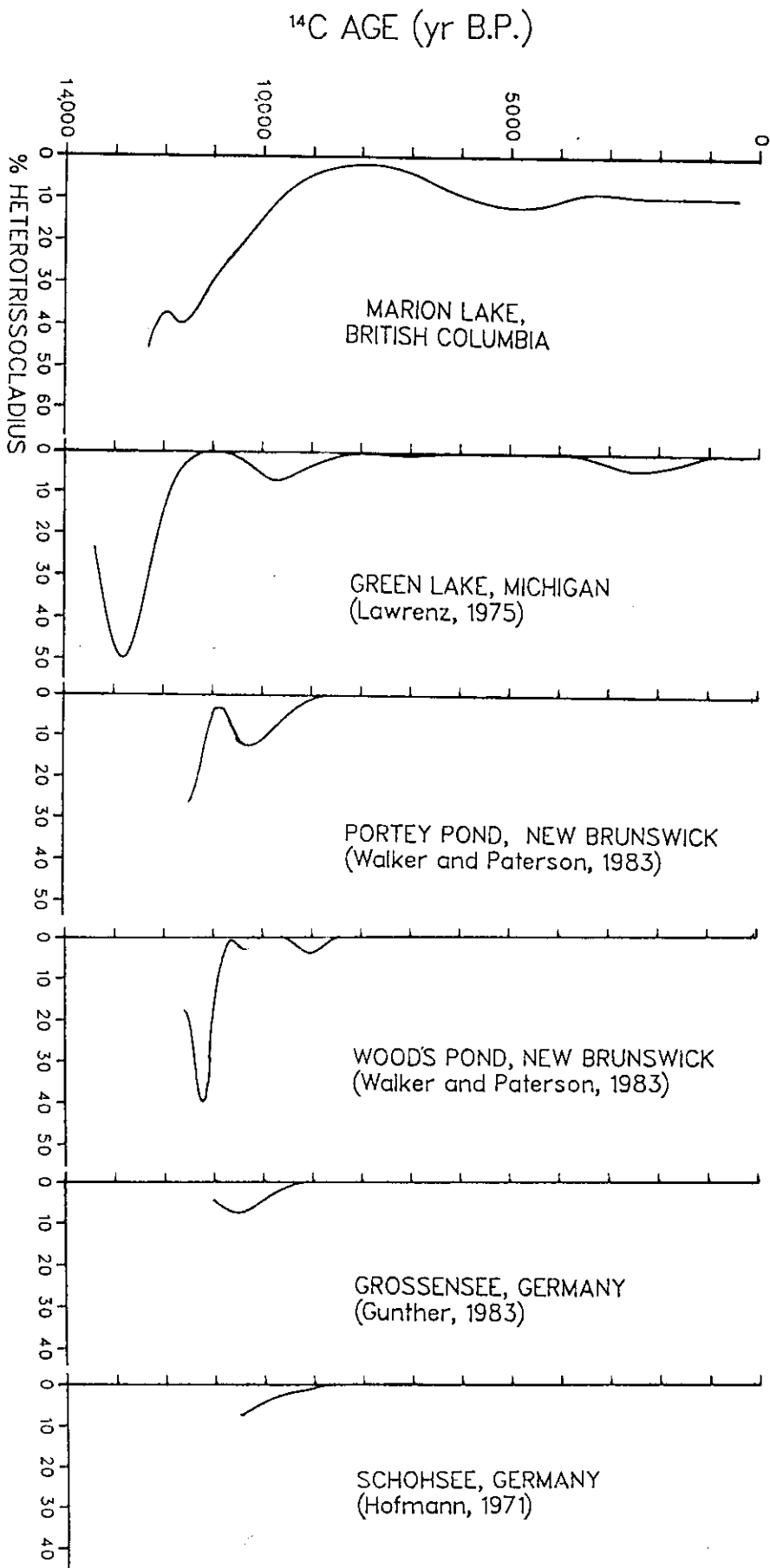


Figure 2.5 Holarctic trends in the postglacial abundance of *Heterotrissocladius* in temperate lakes.

probably climate, is being exerted upon these faunas. This stimulus does not coincide with the arrival of forest, but may precede forest development as in New Brunswick, or follow, as at Marion Lake. Because those sites where a late-glacial *Heterotrissocladius* community has been recorded are widely separated, the evidence suggests a widely distributed *Heterotrissocladius* fauna in lakes near the ice margins. With rising temperatures this fauna retreated to its present distribution in arctic-alpine regions and to the deep-waters of large oligotrophic temperate lakes.

As described above, the large temperature changes inferred near the Pleistocene/Holocene boundary probably account for the major faunal changes. Subsequent Holocene succession is not clearly climatically related. However, *Heterotrissocladius* declines to minimum numbers at Marion Lake during the inferred xerothermic interval (10,000 to 7000 yr B.P.: Mathewes and Heusser, 1981; Mathewes, 1985). The subsequent post-Mazama increase in *Heterotrissocladius* could also record a palaeoclimatic response. *Corynocera*, another element often associated with cool waters (Fjellberg, 1972; Moore, 1978), and late-glacial climates (Andersen, 1938; Hofmann, 1978, 1983a, b; Schakau and Frank, 1984) is also prominent in the post-Mazama sediments.

One might argue that a gradual oligotrophication of Marion Lake occurred through the Holocene, yet Marion Lake is so dependent upon allochthonous and littoral (epipelagic algal and macrophytic) production (Efford and Hall, 1975) that planktonic photosynthesis may have little relevance. Littoral production would not have decreased as the lake shallowed. Also, given that Marion Lake's sediments are predominantly (by volume) allochthonous organic tissues, sedimentation rates may reflect allochthonous inputs. The radiocarbon chronology provided by Mathewes' (1973) indicates relatively rapid post-Mazama sedimentation. This rapid sedimentation would indicate greater allochthonous inputs following 6800 yr B.P. Such an effect would not explain the observed Holocene chironomid succession.

It should be noted, however, that both *Heterotrissocladius* species presently inhabiting Marion Lake (*H. marcidus* and *H. latilaminus* Sæther: Sæther, 1975b) belong to the more warm-adapted *H. marcidus* group. The more cold-stenothermal *H. subpilosus* group is often associated with *Parakiefferiella* sp.A (Sæther, 1970; Sæther and McLean, 1972; Hare, 1976). Günther (1983) records only *H. subpilosus* in the late-glacial of his German site. Thus the late-glacial and Holocene faunas of Marion Lake may not include the same *Heterotrissocladius* species.